

REVIEW

Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors

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ABSTRACT

1. We reviewed worldwide spatial patterns in the food habits of the brown bear *Ursus arctos* in relation to geographical (latitude, longitude, altitude) and environmental (temperature, snow cover depth and duration, precipitation, primary productivity) variables.
2. We collected data from 28 studies on brown bear diet based on faecal analysis, covering the entire geographical range of this widely distributed large carnivore. We analysed separately four data sets based on different methods of diet assessment.
3. Temperature and snow conditions were the most important factors determining the composition of brown bear diet. Populations in locations with deeper snow cover, lower temperatures and lower productivity consumed significantly more vertebrates, fewer invertebrates and less mast. Trophic diversity was positively correlated with temperature, precipitation and productivity but negatively correlated with the duration of snow cover and snow depth. Brown bear populations from temperate forest biomes had the most diverse diet. In general, environmental factors were more explicative of diet than geographical variables.
4. Dietary spatial patterns were best revealed by the relative biomass and energy content methods of diet analysis, whereas the frequency of occurrence and relative biomass methods were most appropriate for investigating variation in trophic diversity.
5. Spatial variation in brown bear diet is the result of environmental conditions, especially climatic factors, which affect the nutritional and energetic requirements of brown bears as well as the local availability of food. The trade-off between food availability on the one hand, and nutritional and energetic requirements on the other hand, determines brown bear foraging decisions. In hibernating species such as the brown bear, winter severity seems to play a role in determining foraging strategies. Large-scale reviews of food habits should be based on several measures of diet composition, with special attention to those methods reflecting the energetic value of food.

Keywords: biogeographical variation, climate change, global warming, Normalized Difference Vegetation Index (NDVI), snow cover

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INTRODUCTION

Understanding food habits is crucial to understanding the ecology of species. Diet influences many ecological and life-history traits, such as spatial distribution, social and foraging behaviour, body mass and reproduction (Gittleman 1985, Iriarte et al. 1990, Welch et al. 1997, Swenson et al. 1999, Gende & Quinn 2004, Swenson et al. 2007). Feeding is commensurate in the long term with fitness and, thus, it is a target for natural selection (Schoener 1971). Diet studies at local scales, especially those based on long-term research, have contributed substantially to a better knowledge of the diet-mediated factors influencing ecological traits (e.g. Jędrzejewska & Jędrzejewski 1998, Naves et al. 2006, Schmidt 2008). However, a complete view of a species' feeding ecology requires identifying the factors affecting its feeding behaviour throughout its geographical range. This biogeographic approach may also contribute to understanding the potential changes in ecological traits of a given species as a response to global changes.

Geographic variables, in particular latitude, have classically received the most attention in biogeography. One of the oldest biogeographical patterns in ecology is the latitudinal species diversity gradient (Pianka 1966). More recently, factors other than latitude have been shown to play important roles in shaping biogeographical patterns (Hawkins & Diniz-Filho 2004, Gaston et al. 2008). For instance, climate, and especially temperature, can have profound effects on various biogeographical patterns at intraspecific, interspecific and assemblage levels (Gaston 2000, Gaston et al. 2008). Geographical variation in ecological and life-history traits of mammals, and of herbivorous mammals in particular, have also successfully been linked with different measures of vegetation biomass and net primary productivity, like the Normalized Difference Vegetation Index (NDVI, reviewed in Pettorelli et al. 2005, Mueller et al. 2008). Although geographical patterns in feeding habits may be better explained by environmental factors, the majority of studies of biogeographical variation in diet has been focused on latitudinal patterns (e.g. Iriarte et al. 1990, Virgós et al. 1999, Clavero et al. 2003, Zalewski 2004, Lozano et al. 2006).

An important issue, though rarely acknowledged in analyses of patterns in the feeding habits of a species, is the method used to assess the diet. The majority of reviews are based on the relative frequency of food items (e.g. Clavero et al. 2003, Lozano et al. 2006). However, the relative frequency of occurrence method overestimates the importance of small and trace food items and under-represents very digestible food (such as meat) and items consumed massively in certain periods (Reynolds & Aebischer 1991). The relative volume or weight of food items can also give biased results due to the big differences in the digestibility of food items. Biomass and energy estimates are considered more appropriate and sensitive for ecological interpretation (Hewitt & Robbins 1996).

A model species for studying the influence of environmental and geographical factors on feeding habits is the brown bear *Ursus arctos*. It is one of the most widespread large carnivores in the world. It has a circumpolar distribution that historically included most of the Holarctic (Pasitschniak-Arts 1993). Environmental conditions vary markedly over its range, as brown bears occupy a wide variety of habitats from tundra to temperate forests. The species' high level of ecological flexibility is determined by its extremely broad diet range (Krechmar 1995). Brown bears have evolved a generalist omnivore strategy. Although they possess all the morphological traits of carnivores, in many ecosystems their diet comprises primarily

plant matter, which makes understanding their feeding ecology very challenging (Robbins et al. 2004, Sacco & Van Valkenburgh 2004).

Food habits are pivotal in brown bear ecology and behaviour (Welch et al. 1997, Swenson et al. 1999, Gende & Quinn 2004). The availability and quality of food have strong influences on brown bears' population dynamics: they affect the age at first reproduction, litter size, breeding interval, body size, population density, home range and habitat selection (Stringham 1986, Blanchard 1987, Stringham 1990, Palomero et al. 1997, Welch et al. 1997, Hilderbrand et al. 1999a, Ferguson & McLoughlin 2000, McLoughlin 2000, Nomura & Higashi 2000). Brown bears' diet has to meet the demands of maintenance, growth, cub rearing, and the accumulation of lipid stores required for winter dormancy, gestation and lactation (Hilderbrand et al. 1999b, Robbins et al. 2007). In order to maximize their growth and fat accumulation, brown bears must balance their energy and nutrient intake according to the most efficient foraging strategy for their body size, thus choosing between a completely frugivorous or a mixed diet (Welch et al. 1997, Rode & Robbins 2000, Rode et al. 2001, Felicetti et al. 2003, Robbins et al. 2007).

Previous reviews on brown bear diet have revealed some latitudinal trends in their food composition in relation to carnivory (Elgmork & Kaasa 1992, Vulla et al. 2009) and myrmecophagy (Swenson et al. 1999, Große et al. 2003). Elgmork and Kaasa (1992) described an increase in the share of meat in brown bear diet at higher latitudes, but they did not test this relationship statistically. More recently, Vulla et al. (2009) corroborated the significance of the previous finding by Elgmork and Kaasa (1992), but their review included only European studies, thus leaving an important gap in the data set from most of the species' range.

In this study, we review the food habits of brown bears over their entire geographical range and search for biogeographical patterns in diet composition and diversity, taking into account the methods of diet assessment. Specifically, we aimed: (i) to document spatial variation in the diet composition of the brown bear over its geographical range; (ii) to assess which geographical, climatic and biotic factors best explain biogeographical patterns in diet composition and diversity; and (iii) to evaluate the appropriateness of the different methods of diet assessment for the study of biogeographical variation in food habits.

MATERIALS AND METHODS

Review of diet studies

We reviewed 38 publications on brown bear diet revealed by faecal analyses. In order to standardize the database, we applied certain criteria for the selection of studies. We excluded from the database all the studies that are as follows: (i) did not cover all seasons (i.e. the entire year) of brown bears' activity; (ii) had food categories, which we considered too wide; (iii) had a sample size smaller than 95 scats; or (iv) had insufficient data to calculate the following diet estimates: relative frequency of occurrence, percentage of volume or dry weight of food categories. As a result, we selected data from 28 studies for the analyses (see Appendix 1). The geographical location of these studies is shown in Fig. 1 and covers the geographical range of the species, i.e. Eurasia and North America. We pooled the data from studies conducted in exactly the same area but in different years. In the study of Krechmar (1995), which included different study areas, we treated each one independently.

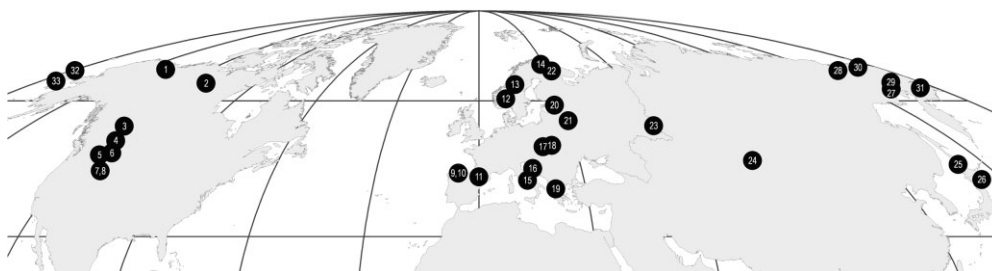


Fig. 1. World map showing the study areas of the reviewed papers, numbered as follows (see Appendix 1): 1: MacHutchon and Wellwood (2003), 2: Gau et al. (2002), 3: Munro et al. (2006), 4: McLellan and Hovey (1995), 5: Servheen (1983), 6: Mace and Jonkel (1985), 7: Mattson et al. (1991), 8: Mealey (1980), 9: Clevenger et al. (1992), 10: Naves et al. (2006), 11: Berducou et al. (1983), 12: Elgmork and Kaasa (1992), 13: Dahle et al. (1998), 14: Persson et al. (2001), 15: Zunino and Herrero (1972), 16: Cincjak et al. (1987), 17: Rigg and Gorman (2005), 18: Frąckowiak (1997), 19: Vlachos et al. (2000), 20: Vulla et al. (2009), 21: Sidorovich (2006), 22: Semenov-Tian-Shanskii (1972), 23: Sharafutdinov and Korotkov (1976), 24: Grachev and Fedosenko (1977), 25: Ohdachi and Aoi (1987), 26: Sato et al. (2004), 27: Chernjavskij and Petrichenko (1984), 28–33: Krechmar (1995).

The selected studies varied in the way the contribution of different food items to brown bear diet was assessed: by frequency of occurrence, percentage of volume, percentage of dry weight, estimated biomass consumed, dietary energy content, or by several of these estimates (Appendix 1). We divided the data presented in the reviewed studies accordingly into four data sets:

1. Relative frequency of occurrence (RFO, 23 studies covering 27 different study areas, Appendix 2): the number of occurrences of a certain food item expressed as a percentage of the total number of occurrences of all food items considered.
2. Relative volume (RV, 19 studies covering 17 different study areas, Appendix 3): the relative volume (%) of a certain food category of the total volume of all scats. Two studies in which the diet content was reported as relative weight and as an index of relative contribution, respectively, were also included in this data set.
3. Relative biomass of consumed food items (RB, 17 studies covering 15 different study areas, Appendix 4): the percentage biomass of a given food category of the total biomass consumed. For the studies in which only volume values and not biomass were reported, we calculated the relative biomass on the basis of the relative volume using the correction factors proposed by Hewitt and Robbins (1996).
4. Relative energy content of consumed food items (RE, 17 studies covering 15 different study areas, Appendix 5). We obtained data on estimated dietary energy content by multiplying the relative biomass values of food items by their energy correction factors (Persson et al. 2001). We then calculated the relative energy content from the total energy.

We considered seven food categories: green vegetation, fleshy fruits, hard mast (hazelnuts, beechnuts, acorns and coniferous tree seeds), invertebrates, vertebrates, cereal bait (including corn and other vegetables used for ungulate baiting) and others (wood, pebbles, garbage, unidentified fraction). We did not consider aquatic vertebrates, namely fish, as a separate category because they occurred in brown bear diet only in three of the selected studies. Moreover, adding the category fish did not improve the significance of the results. Some researchers did not present bear diet

composition year-round; in those cases, we estimated the annual values by averaging the seasonal percentages of food categories, weighed by the number of scats analysed in each season.

Explanatory variables and statistical analysis

We estimated the latitude and longitude of each location with 0.1° resolution and assigned negative values of longitude to the Western Hemisphere. Data on mean altitude and precipitation were downloaded from WORLDCLIM database (<http://www.worldclim.org/current>) and extracted for all study areas. We calculated the mean precipitation (mm) in the bears' active period for their entire geographical range (April–October) from the monthly averages for 1950–2000. We used NDVI values as a measure of primary productivity of the study areas. Data on NDVI were obtained from the Global Inventory Monitoring and Modelling Studies data set, which consists of mean NDVI values for 15-day periods with a spatial resolution of approximately $8 \times 8 \text{ km}^2$, available at <http://glcf.umiacs.umd.edu/data/gimms/> (Pinzon et al. 2005, Tucker et al. 2005). The bimonthly NDVI values were averaged for the period 1982–2000 for the whole surface of each study site for the period of bears' activity (April–October).

We obtained satellite-derived data on snow cover (monthly snow cover and snow depth) from the Global Ecosystem Database version 2.0 (downloaded from the NOAA National Geophysical Data Center, 325 Broadway, Boulder, Colorado, USA, Website <http://www.ngdc.noaa.gov>) following Bartoń and Zalewski (2007, data from October 1978 to August 1987). From these data, we calculated the mean annual length of the period with snow cover (mean number of months with snow cover > 0 cm) and the mean snow depth (cm) from November to March. Average monthly temperature values for the years 1970–2000 were taken from the NCEP/NCAR Reanalysis Database (<http://www.cdc.noaa.gov/data/reanalysis/reanalysis.shtml>). We calculated average values of temperature, precipitation, NDVI and altitude for each study site by using geographical information system software (ArcGIS version 9.2, ESRI, Inc., Redlands, CA, USA, Anonymous 2006).

According to the vegetation maps by Eyre (in Strahler & Strahler 1987), we assigned each location to one of the three following biomes: (i) tundra (both arctic and alpine); (ii) boreal and coniferous forest; and (iii) temperate deciduous and mixed forest. We also calculated trophic diversity using the Shannon–Wiener index H' (Weaver & Shannon 1949) applied separately to each of the four data sets (RFO, RV, RB and RE) for all the locations.

We performed a principal component analysis (PCA) to reveal patterns in brown bear diet that could not be found by analyzing each variable separately, and to reduce the six main food categories into three orthogonal factors. We analysed the four databases separately (RFO, RV, RB and RE). We used the covariance matrix, which is appropriate when the variables are measured in the same units and when the aim is to strengthen the differences in variance for each variable in the analysis (Quinn & Keough 2006). Arcsine transformation of the variables did not improve significantly their normality or the results from PCA, so we used raw data. Depending on data normality, we used Spearman or Pearson correlations to investigate relationships between the PCA factors, trophic diversity and geographical and environmental variables (latitude, longitude, mean altitude, mean temperature, mean precipitation, mean NDVI, duration of snow cover and mean snow depth). We did

not apply the Bonferroni correction because we consider it unnecessarily conservative, and it greatly inflates Type II errors (Moran 2003). The significance level was set at 0.05.

We used the *G*-test for homogeneity of percentages to check whether the different methods of diet assessment generated significantly different results in the share of the six main food categories of plant and animal food. We used a two-way ANOVA to test whether trophic diversity (H') and the PCA factors were related to the type of biome. Only the significant results are described in the text. All statistical analyses were performed in STATISTICA 8.0 (StatSoft, Inc., Tulsa, OK, USA, Anonymous 2007).

RESULTS

Patterns in diet composition

The PCA using the six main food categories generated five orthogonal factors. The first two and three factors explained more than 72% and 88% of the variance of the original variables in all data sets, respectively (Table 1). The main gradient defined by PCA factors separated brown bear populations in which vertebrates represented the bulk of the diet from more herbivorous populations. Vertebrates were more relevant (first PCA factor) when considering biomass or energy. In the RFO and RV data sets, a first gradient from populations with a high proportion of green vegetation in their diets to those that were more frugivorous, relying on fleshy and hard fruits, was defined. PCA factors also distinguished populations for which mast was an important component of the diet, especially in terms of biomass and energy. Invertebrates had some relevance, only appearing as a third factor in the RFO and RE data sets (Table 1).

Environmental variables correlated better with the gradients defined by PCA factors than with geographical variables. The consumption of vertebrates by brown bears (factor 2 in RFO and RV data sets and factor 1 in RB and RE data sets) increased significantly with increases in the duration of snow cover and snow depth but decreased with increasing temperatures, precipitation and NDVI (Table 2, Fig. 2). The consumption of fleshy fruits (factor 2 in RFO data set) was positively correlated with temperature and NDVI. Similarly, the share of hard mast in brown bear diet (factor 2 in RV and RB data sets and factor 1 in RE data set) was significantly higher at warmer temperatures, higher precipitation, higher NDVI and lower snow cover (duration and depth). Consumption of invertebrates (factor 3 in RFO data set) followed the same pattern. The share of green vegetation in the diet did not relate to mean NDVI, but it was significantly higher in colder areas and in locations with longer snow periods (factor 2 in RB data set, Table 2).

Geographical variables themselves did not explain much, and the patterns revealed were a repetition of those explained by environmental variables (Table 2). Thus, brown bear populations at higher latitudes consumed more vertebrates, fewer fruits and less hard mast (factor 2 in RFO and RV data sets, and factor 1 in RE data set). Longitude was correlated with the consumption of green vegetation, mast and invertebrates (factor 1 in RV data set, factor 2 in RB data set, factor 3 in RE data set). Hard mast and insects appeared to be more important for Eurasian brown bears than for North American populations, whereas brown bears in America consumed significantly more green vegetation (Table 2).

Brown bear diet varied significantly among different biogeographic regions (Fig. 3). The consumption of vertebrates was highest in the tundra and lowest in

Table 1. Results from the principal component analysis of the brown bear diet expressed as relative frequency of occurrence, relative volume, relative biomass, and relative energy. Eigenvalues and variance explained (%) by each PCA factor as well as the correlations (loadings) between PCA factors and main food categories in brown bear diet are indicated

Variables	Relative frequency of occurrence			Relative volume			Relative biomass			Relative energy		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Green vegetation	-0.96	0.05	-0.27	-0.99	0.10	-0.03	0.38	0.71	0.59	0.08	0.68	0.63
Fleshy fruits	0.61	0.64	-0.42	0.58	-0.40	0.65	0.37	0.54	-0.61	0.23	0.78	0.12
Hard mast	0.28	0.26	0.22	0.34	-0.67	-0.65	0.41	-0.89	0.13	0.76	-0.65	0.08
Invertebrates	-0.14	0.11	0.85	0.06	-0.09	0.46	0.21	0.27	-0.44	0.15	0.51	-0.65
Vertebrates	0.38	-0.89	-0.24	0.53	0.83	-0.17	-0.99	-0.08	0.06	-0.95	-0.30	0.02
Cereal bait	0.10	0.16	0.66	0.17	-0.27	-0.06	0.37	-0.12	-0.21	0.43	0.21	-0.55
Eigenvalue	329.9	220.3	122.5	551.8	241.3	111.8	727.9	503.5	171.4	827.4	376.1	94.8
Variance explained (%)	43.1	28.8	16.0	57.1	25.0	11.6	46.8	32.4	11.0	59.0	26.8	6.8

PCA, principal component analysis.

Table 2. Correlations of latitude (°), longitude (°), mean altitude (m a.s.l.), mean annual temperature (°C), duration of snow cover (months), mean depth of snow cover (cm), mean precipitation (mm) in April–October and mean NDVI in April–October of the study areas with the PCA factors of different data sets (RFO, RV, RB, RE)

Variable	RFO			RV			RB			RE		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Latitude	n.s.	-0.40*	n.s.	n.s.	0.58*	n.s.	n.s.	n.s.	n.s.	-0.58*	n.s.	n.s.
Longitude	n.s.	n.s.	n.s.	0.58*	n.s.	n.s.	n.s.	-0.54*	n.s.	n.s.	n.s.	-0.63*
Altitude	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Temperature	n.s.	0.50**	0.42*	n.s.	-0.76***	n.s.	0.61*	-0.55*	n.s.	0.72***	n.s.	n.s.
Snow duration	n.s.	n.s.	-0.57***	n.s.	0.51*	n.s.	n.s.	0.58*	n.s.	-0.57*	n.s.	n.s.
Snow depth	n.s.	n.s.	-0.39*	n.s.	0.73***	n.s.	-0.57*	n.s.	n.s.	-0.71***	n.s.	n.s.
Precipitation	n.s.	n.s.	0.56***	n.s.	-0.57*	n.s.	n.s.	n.s.	n.s.	0.53*	n.s.	n.s.
NDVI	n.s.	0.50**	0.60***	n.s.	-0.72***	n.s.	0.64*	n.s.	n.s.	0.63*	n.s.	n.s.

PCA, principal component analysis; NDVI, Normalized Difference Vegetation Index; RFO, relative frequency of occurrence; RV, relative volume; RB, relative biomass; RE, relative energy; n.s., not significant.

The *r*-values are from Pearson correlations except for those in italics, which are from Spearman correlations.

Significance codes: *** $P < 0.005$, ** $P < 0.01$, * $P < 0.05$.

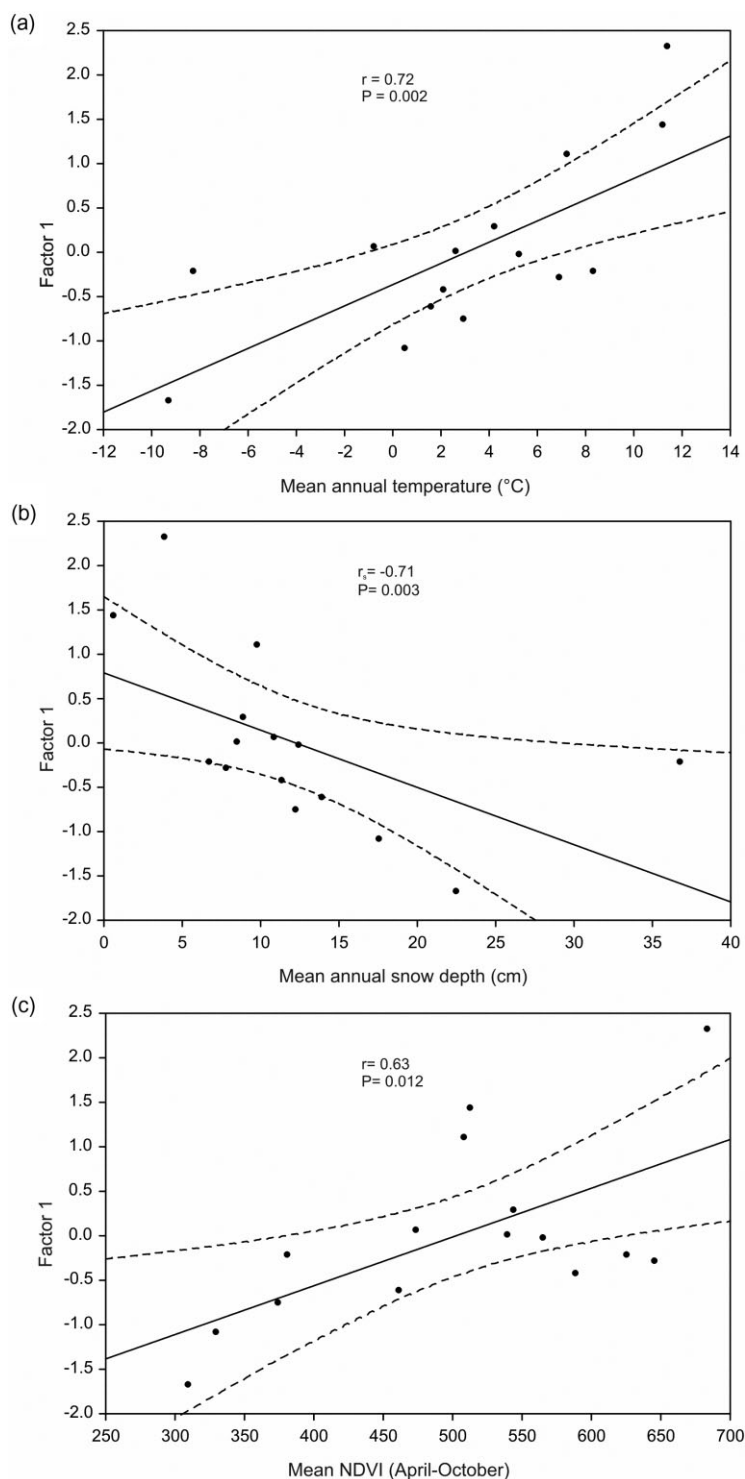


Fig. 2. Relationships between principal component analysis factor 1 of the dietary energy content data set and (a) mean annual temperature (°C), (b) mean annual snow depth (cm), and (c) mean NDVI in the period April–October ($n = 15$). NDVI, Normalized Difference Vegetation Index.

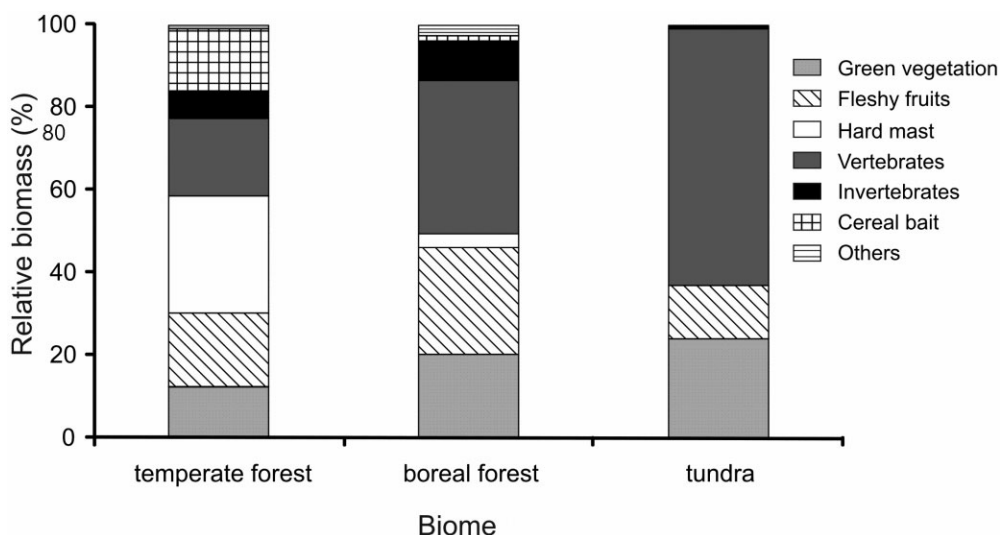


Fig. 3. Contribution of the seven food categories in brown bear diet (assessed as relative biomass, RB data set) in different biogeographic regions ($n = 15$).

temperate forest biomes, while fruits and hard mast showed the opposite pattern ($F_{2,24} = 3.91$, $P = 0.034$, factor 2 in RFO data set, $F_{2,14} = 5.29$, $P = 0.019$, factor 2 in RV data set, and $F_{2,12} = 5.74$, $P = 0.018$, factor 1 in RE data set). The contribution of invertebrates to brown bear diet was the highest in temperate forest and the lowest in tundra biome ($F_{2,24} = 5.55$, $P = 0.010$, factor 3 in RFO data set).

Dietary diversity

In general, brown bear trophic diversity correlated better with environmental variables than with geographical variables (Table 3). The trophic diversity index H' was positively correlated with temperature, precipitation, and NDVI, and negatively correlated with duration of snow cover and snow depth. In the RV data set, we also observed a strong positive relationship with longitude. Thus, brown bear trophic diversity was higher in warmer locations with less snowy winters, higher precipitation, higher NDVI and in Eurasia. In terms of energy, no significant correlations were found except with precipitation and NDVI (Table 3). Trophic diversity was significantly different among biogeographic regions in three data sets ($F_{2,24} = 4.26$, $P = 0.026$, RFO data set, $F_{2,14} = 4.011$, $P = 0.042$, RV data set, $F_{2,12} = 4.741$, $P = 0.030$, RB data set). Trophic diversity was the highest at locations within the temperate forest region, showed intermediate values for boreal and coniferous forests and was lowest at locations within the tundra biome (mean H' values \pm SD for the three biomes in RFO data set: 1.15 ± 0.163 , 1.30 ± 0.273 , 1.47 ± 0.218 , respectively).

Methods of diet assessment

The share in brown bear diet of the different food categories was significantly different among the four methods of diet assessment ($G = 65.803$, d.f. = 18, $P < 0.001$, Fig. 4). Green vegetation and fleshy fruits were the dominant food items when the RFO and RV methods were used. When the diet was assessed with RB or RE,

Table 3. Spearman correlations of trophic diversity H' with geographic variables [latitude (°), longitude (°), mean altitude (m a.s.l.) and environmental variables [mean annual temperature (°C), duration of snow cover (months), mean depth of snow cover (cm), mean precipitation (mm) in April–October and mean NDVI in April–October] of the study areas

Method	Latitude	Longitude	Altitude	Temperature	Snow duration	Snow depth	Precipitation	NDVI
RFO	n.s.	n.s.	n.s.	0.48*	−0.54***	−0.48*	0.69***	0.57***
RV	n.s.	0.84***	n.s.	n.s.	−0.55*	n.s.	0.60*	0.53*
RB	n.s.	n.s.	n.s.	0.72***	−0.75***	−0.58*	0.65*	0.70***
RE	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.60*	0.60*

NDVI, Normalized Difference Vegetation Index; RFO, relative frequency of occurrence; RV, relative volume; RB, relative biomass; RE, relative energy; n.s., not significant.
Significance codes: *** $P < 0.005$, * $P < 0.05$.

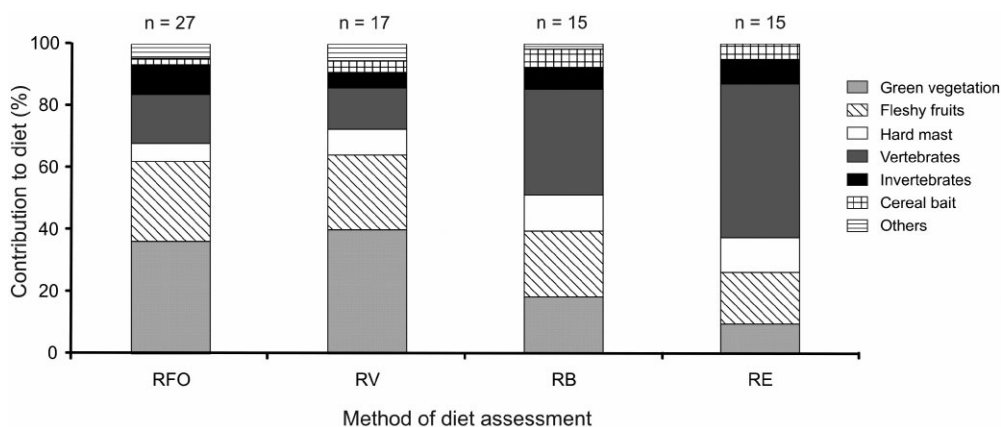


Fig. 4. Contribution of the seven food categories to the diet of the brown bear throughout its range, reported as percentage of relative frequency of occurrence (RFO), percentage of relative volume (RV), percentage of consumed biomass (RB) and percentage of dietary energy content (RE). n, number of study areas.

vertebrates constituted the bulk of the diet (Fig. 4). In general, the vegetal component of the brown bear diet was significantly better represented (more than 70%) when using RFO or RV methods, whereas diet estimations in terms of biomass or energy (RB, RE) yielded more similar proportions of plant and animal food items in the diet ($G = 505.805$, d.f. = 3, $P < 0.001$).

DISCUSSION

The geographical variation in brown bear food habits may be partly explained by differences in the availability of food resources, which, in turn, relate to climatic and biotic conditions. For instance, the differences in the contribution of mast and fleshy fruits to brown bear diet among regions are mainly due to the lack of hard mast and large soft mast, such as tree fruits, in the coldest areas, and their abundance in the temperate zone. The higher abundance and availability of fruits and insects in warmer regions is reflected in the diet of many omnivorous species (e.g. Virgós et al. 1999, Zalewski 2004, Lozano et al. 2006, Rosalino & Santos-Reis 2009). The availability of ants is highest in the boreal forest, where brown bears intensively consume them (Swenson et al. 1999); in warmer locations, other groups of insects (mainly bees and wasps) became more important in their diet. Similarly, the higher consumption of vertebrates in colder locations with deep snow cover and in less productive regions, as tundra, can be partly explained by the abundance of ungulate carcasses and by facilitated predation on ungulates at the end of winter and in early spring when the energy reserves of ungulates are depleted (Green et al. 1997, Jędrzejewska & Jędrzejewski 1998, Selva et al. 2005) together with the lower availability of vegetal bear food (Wiegand et al. 2008).

Satellite-derived measures of plant productivity, like NDVI, perform well in explaining variations in species life-history traits, particularly in ungulates (e.g. Melis et al. 2006, Pettorelli et al. 2006, Mueller et al. 2008). However, researchers studying traits of carnivores with an omnivorous diet have often failed to find a similar relationship (Bartoń & Zalewski 2007, Melis et al. 2010, Zhou et al. 2011). NDVI may not accurately

reflect the quality of forage for herbivores (e.g. Mueller et al. 2008) or the abundance of some food, like fruits or mast, for omnivore species (e.g. Camarero et al. 2010, Zhou et al. 2011). Our study is the first showing a dietary pattern associated with NDVI in an omnivore. But surprisingly in our study, NDVI did not relate to the consumption of green vegetation, but to that of meat. This may be explained by bears compensating for the limited availability of vegetal food by consuming more vertebrates, and by NDVI (which is highly correlated with climate, Stenseth et al. 2002) mirroring the correlations among PCA factors and climatic conditions. As suggested for other generalist carnivores in the Palearctic (Bartoń & Zalewski 2007, Melis et al. 2010, Zhou et al. 2011), food availability may be better explained by climatic factors.

Brown bear diet depends not only on food availability but also on the trade-offs imposed by the nutritional and energetic requirements of bears (Welch et al. 1997, Rode & Robbins 2000, Rode et al. 2001, Felicetti et al. 2003, Robbins et al. 2007). The digestible energy and protein content vary significantly among bear food items: meat contains the highest values (Pritchard & Robbins 1990, Welch et al. 1997, Felicetti et al. 2003, Robbins et al. 2007). Felicetti et al. (2003) found that brown bears consuming high-protein diets gained mainly lean mass, whereas brown bears on low-protein diets gained primarily fat. Lean mass gain occurs in brown bears mainly after hibernation, in spring, when they need to rebuild their muscles. This process is particularly important in northern areas, where brown bears hibernate for twice as long and lose more weight than those in more southern areas (Swenson et al. 2007). Thus, to optimize their energetic balance and mass growth, brown bears in areas with longer winters should select a protein-rich diet (Swenson et al. 2007, Vulla et al. 2009). Our results support this hypothesis.

Larger brown bears, which have higher energetic needs and are more constrained by foraging time, benefit from more carnivorous diets (Welch et al. 1997, Hilderbrand et al. 1999b, Rode & Robbins 2000, Rode et al. 2001, Robbins et al. 2007). Larger animals cope better in cool climates due to the reduction of the surface area to volume ratio (Bergmann 1847). However, brown bears do not follow Bergmann's rule (Swenson et al. 2007) and, thus, the latitudinal (Elgmork & Kaasa 1992, Vulla et al. 2009) and environmental (this study) gradient found in carnivory cannot be explained by a morphological adaptation (increase in body size). The increased consumption of animal prey in northern latitudes has also been found in the badger *Meles meles* and the genus *Martes* (Vulla et al. 2009, Zhou et al. 2011). The authors explain this pattern as an adaptation to harsh climates and as result of the lower availability of plant items in northern latitudes. We suggest that this may also be related to the phenomenon of winter inactivity in some mammals, which involves a greater loss of body mass in cool climates and a higher need to ingest high-quality food quickly when becoming active. In hibernating mammals, low temperatures and deep snow cover in spring negatively affect the amount of fat deposited (e.g. Melis et al. 2010).

According to the latitudinal gradient in diversity (Rosenzweig 1995), we could expect an increased trophic diversity of the brown bear in southern latitudes, as found for other generalist predators (Iriarte et al. 1990, Virgós et al. 1999, Clavero et al. 2003, Zalewski 2004, Lozano et al. 2006). However, brown bear dietary diversity did not relate to latitude but to climatic conditions, primary productivity and the type of biome. In fact, most of the authors cited above found a weak and not always significant correlation between latitude and dietary diversity and also concluded

that the biome type was the most important factor explaining diversity in trophic habits (Virgós et al. 1999, Lozano et al. 2006). Longitude, which is indicative of the degree of seasonality and winter severity (Meiri et al. 2005), explained more variation in brown bear diet than other geographical factors. The lower trophic diversity and the low contribution of mast and insects to the diet of brown bears in North America may be the result of lower average temperatures and higher winter severity in comparison with European locations of the same latitude.

Therefore, our findings are consistent with the idea that environmental factors explain species' spatial patterns better than geographical variables, in spite of positional variation (e.g. latitude, altitude, longitude) and environmental variation (e.g. temperature, precipitation, productivity) being highly correlated (e.g. Gaston 2000, Hawkins & Diniz-Filho 2004, Gaston et al. 2008). We demonstrate that when using geographical variables as a proxy of environmental variables or climatic components, some spatial patterns may be missed or misunderstood. The study on brown bear diet by Aichun et al. (2006) in the Qinghai–Tibetan Plateau, China, is very illustrative. The latitudinal gradient would predict a high dietary diversity there, at 35°N. However, brown bear diet consists almost entirely of meat, a result that may be explained by the harsh environmental conditions in the area (extremely low temperatures and productivity, and deep snow) and thus supports our findings.

Temperature and snow conditions are among the most important factors affecting the feeding ecology of the brown bear. Both have been given as the main factors explaining biogeographical variation in traits, including diet, of other omnivores (Melis et al. 2006, Bartoń & Zalewski 2007, Melis et al. 2010, Zhou et al. 2011). Therefore, it may be expected that climate change will greatly affect brown bear food habits through changes in food availability, hibernation patterns, nutritional and energetic demands, and foraging behaviour. Globally increasing temperatures are yielding shorter winters with less snow, especially in northern latitudes and higher elevation areas (Sagarin & Micheli 2001, Wilmers & Post 2006). Early snow melt substantially reduces the amount of late-winter and early-spring carrion, which is vital for bears after hibernation and until other food resources become available (Wilmers & Post 2006). Climate change may affect brown bear feeding habits also through changes in plant distribution and phenology. As a response to warmer temperatures, Rodríguez et al. (2007) documented a long-term decrease in the contribution of boreal and temperate food items in brown bear diet during the hyperphagic season, when brown bears typically consume high amounts of fruit to accumulate fat for winter dormancy and for successful reproduction. Changes in the timing and intensity of fruiting and ripening of fruit and mast, and declines in the availability of high-quality fruits, such as *Vaccinium* sp., may have important consequences for brown bear population dynamics (Rodríguez et al. 2007). If key brown bear food resources disappear without the corresponding change in the timing of alternative food resources, a serious food bottleneck could develop.

Diet reviews at large spatial scales may yield quite different outputs depending on the method of diet estimation. The large discrepancy in the digestibility and energy content of food items, especially of trophic generalists, greatly contributes to this. In the case of brown bears, despite the large vegetative component in their diet and their morphological adaptations for herbivory, their digestive capabilities are those of obligate carnivores, thus they digest meat efficiently, but cellulose poorly (Bunnell & Hamilton 1984, Pritchard & Robbins 1990, Hewitt & Robbins

1996). By giving the same importance to all food items present in the diet, the RFO failed to reveal some relationships or showed weaker correlations than other methods. RFO and RE performed well to investigate patterns in the consumption of small food items or items not consumed in big amounts, like invertebrates. All methods of diet assessment are somehow inaccurate and inflicted with some errors; thus, whenever possible, several measures should be used to get a complete picture (Jędrzejewska & Jędrzejewski 1998). Our results suggest that RB and RE best represent the real diet and trophic needs, and have the most ecological meaning. They seem to be the most suitable methods of diet assessment when investigating biogeographical variation in dietary content, whereas RFO and RB are more explicative of patterns in dietary diversity.

To sum up, the diet of the brown bear varies significantly throughout its range, from almost herbivorous to highly carnivorous, highlighting the generalist character of the species. Brown bears optimize diet selection, and thus foraging behaviour, in order to meet different energetic and nutritional requirements while minimizing the energy costs of maintenance. The local availability and abundance of potential food items partly explain brown bear food habits. Climatic variables, also during the hibernating period, best explain the variation in the brown bear diet. Large-scale reviews of food habits based on several measures of diet composition contribute to a better knowledge of species' feeding ecology and can provide insight into their potential response to global changes.

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Appendix 1 Location and biome of the study areas in the reviewed studies, with an indication of the method used by authors (RFO – relative frequency of occurrence, RV – relative volume, RB – relative biomass).

Study area*	Study	Method	Latitude	Longitude	Biome**	Location
1	MacHutchon & Wellwood (2003)	RV, RFO	69.2	-140.1	tundra	Canada
2	Gau et al. (2002)	RV, RFO	64.5	110.5	tundra	Canada
3	Munro et al. (2006)	RB	53.0	-117.0	boreal	Canada
4	McLellan & Hovey (1995)	RV, RFO	49.0	-114.9	boreal	Canada
5	Servheen (1983)	RV	48.3	-114.3	boreal	USA
6	Mace & Jonkel (1985)	RFO	48.3	-113.8	boreal	USA
7	Mattson et al. (1991)	RV	44.6	-110.5	boreal	USA
8	Mealey (1980)	RV, RFO	44.6	-110.5	boreal	USA
9	Clevenger et al. (1992)	RV, RFO	43.3	-5.3	temperate	Spain
10	Naves et al. (2006)	RV, RFO	43.3	-5.3	temperate	Spain
11	Berduco et al. (1983)	RV***	42.6	0.7	temperate	France
12	Elgmork & Kaasa (1992)	RV, RFO, RB	60.5	10.0	boreal	Norway
13	Dahle et al. (1998)	RV, RFO, RB	64.2	14.5	boreal	Norway, Sweden
14	Persson et al. (2001)	RV, RFO, RB	69.7	28.7	boreal	Norway
15	Zunino & Herrero (1972)	RF	42.8	13.9	temperate	Italy
16	Cinjak et al. (1987)	RV, RFO	44.9	15.6	temperate	Croatia
17	Rigg & Gorman (2005)	RV, RFO	49.2	19.9	temperate	Slovakia
18	Frackowiak (1997)	RV, RFO	49.3	22.3	temperate	Poland
19	Vlachos et al. (2000)	RFO	39.9	21.6	temperate	Greece
20	Vulla et al. (2009)	RV, RFO, RB	59.0	26.0	temperate	Estonia
21	Sidorovich (2006)	RFO	55.2	30.2	temperate	Belarus
22	Semenov-Tian-Shanskii (1972)	RFO	67.8	32.0	tundra	Russia
23	Sharafutdinov & Korotkov (1976)	RFO	54.0	58.0	temperate	Russia
24	Grachev & Fedosenko (1977)	RFO	45.4	80.1	boreal	Kazakhstan
25	Ohdachi & Aoi (1987)	RV***	44.9	142.2	boreal	Japan
26	Sato et al. (2004)	RV, RFO	42.8	143.7	boreal	Japan
27	Chernjavskij & Petrichenko (1984)	RFO	64.0	161.8	boreal	Russia
28	Krechmar (1995)	RFO	65.8	159.8	boreal	Russia
29	Krechmar (1995)	RFO	65.6	169.1	tundra	Russia
30	Krechmar (1995)	RFO	65.1	170.6	tundra	Russia
31	Krechmar (1995)	RFO	67.3	170.4	tundra	Russia
32	Krechmar (1995)	RFO	67.9	-177.9	tundra	Russia
33	Krechmar (1995)	RFO	65.0	-173.4	tundra	Russia

*See Fig. 1.

**tundra – alpine and arctic tundra, boreal – boreal and coniferous forest, temperate – temperate deciduous and mixed forest.

***IRC (Index of Relative Contribution, Berduco et al. 1983) or percentage of dry weight (Ohdachi & Aoi 1987).

Appendix 2 Brown bear diet composition, expressed as percentage of the frequency of occurrence (RFO), and trophic diversity (Shannon–Wiener index, H').

Study area*	H'	Green vegetation	Fleshy fruits	Hard mast	Invertebrates	Vertebrates	Cereal bait	Others
1	0.90	69.9	19.5	0.0	1.6	7.1	0.0	1.9
2	1.06	20.7	38.5	0.0	0.0	40.8	0.0	0.0
4	1.10	59.9	23.0	0.0	9.5	7.5	0.0	0.1
6	1.48	46.5	19.8	4.0	13.0	6.5	0.0	10.2
8	0.90	73.1	3.1	2.7	4.7	14.7	0.0	1.7
9, 10	1.51	34.7	20.4	25.4	8.1	11.0	0.0	0.4
12	1.46	32.0	26.0	0.0	8.0	7.0	0.0	27.0
13	1.42	37.0	15.5	0.0	23.2	21.9	0.0	2.4
14	1.59	15.0	19.8	0.0	16.8	23.9	0.0	24.5
15	1.10	47.5	38.2	0.0	10.9	2.0	0.0	1.4
16	1.78	20.1	25.6	21.3	13.4	2.4	10.4	6.8
17	1.59	39.0	27.6	4.2	12.5	4.3	8.7	3.7
18	1.73	26.8	23.9	10.3	4.3	23.3	7.2	4.2
19	1.33	13.4	57.6	13.1	6.8	3.2	5.2	0.7
20	1.41	47.7	11.8	0.0	23.0	7.2	9.0	1.3
21	1.53	25.4	19.6	0.0	32.0	11.1	11.9	0.0
22	1.04	14.0	63.0	0.0	6.0	17.0	0.0	0.0
23	1.27	42.9	25.4	0.0	22.4	9.3	0.0	0.0
24	0.90	57.8	36.4	0.0	0.9	3.5	0.0	1.4
26	1.67	30.0	14.8	6.4	21.6	19.2	8.0	0.0
27	1.30	39.9	37.5	12.4	4.3	5.7	0.0	0.2
28	1.17	25.7	33.6	23.4	3.0	11.4	0.0	2.9
29	1.28	24.7	28.0	20.2	4.5	19.0	0.0	3.6
30	1.32	39.8	17.5	14.4	7.9	14.8	0.0	5.6
31	1.10	25.9	13.2	3.1	0.4	53.6	0.0	3.8
32	1.12	32.7	26.6	0.0	0.0	39.9	0.0	0.8
33	1.38	32.9	13.6	0.0	2.8	36.5	0.0	14.2

*See Fig. 1.

Appendix 3 Brown bear diet composition, expressed as percentage of volume (RV) and trophic diversity (Shannon–Wiener index, H'). Two studies in which the percentage of dry weight and the index of relative contribution respectively were used, are included.

Study area*	H'	Green vegetation	Fleshy fruits	Hard mast	Invertebrates	Vertebrates	Cereal bait	Others
1	0.64	79.6	16.7	0.0	0.8	2.3	0.0	0.6
2	0.92	24.7	13.6	0.0	0.0	61.7	0.0	0.0
3	0.58	84.2	8.9	0.0	1.5	5.3	0.0	0.1
4	1.05	56.5	31.7	0.0	1.6	6.0	0.0	4.2
5	1.16	53.5	23.1	0.0	15.2	8.2	0.0	0.0
7, 8	1.3	58.0	3.5	16.0	4.1	9.8	0.0	8.6
9, 10	1.43	34.0	21.0	32.0	4.0	8.0	0.0	1.0
11	1.29	21.6	38.5	12.9	9.3	15.6	0.0	2.1
12	1.43	24.0	39.0	0.0	8.5	6.5	0.0	22.0
13	1.42	39.4	26.3	0.0	6.6	19.5	0.0	8.2
14	1.43	14.9	34.1	0.0	4.8	32.8	0.0	13.4
16	1.39	18.0	31.0	37.0	1.0	1.0	12.0	0.0
17	1.39	46.1	27.4	2.0	5.0	2.4	15.3	1.8
18	1.7	17.9	28.8	13.8	2.2	23.9	11.1	2.3
20	1.36	50.7	19.2	0.0	7.8	9.0	12.9	0.4
25	1.52	30.9	30.7	15.5	2.9	2.0	0.3	17.7
26	1.82	29.1	17.7	5.9	9.0	16.9	14.0	7.4

*See Fig. 1.

Appendix 4 Brown bear diet composition, expressed as percentage of biomass consumed (RB), and trophic diversity (Shannon–Wiener index, H').

Study area*	H'	Green vegetation	Fleshy fruits	Hard mast	Invertebrates	Vertebrates	Cereal bait	Others
1	1.13	45.3	21.8	0.0	1.9	31.0	0.0	0.0
2	0.3	3.3	3.7	0.0	0.0	93.0	0.0	0.0
3	1.13	58.8	19.1	0.0	2.8	16.3	0.0	3.0
4	1.18	30.2	43.3	0.0	3.3	23.2	0.0	0.0
5	1.37	20.5	31.8	0.0	27.2	20.4	0.0	0.1
7, 8	0.99	10.2	2.1	17.0	3.1	67.6	0.0	0.0
9, 10	1.28	11.1	12.7	55.5	5.3	15.2	0.0	0.2
12	1.28	8.5	45.0	0.0	6.0	34.0	0.0	6.5
13	1.13	19.3	26.6	0.0	13.0	40.5	0.0	0.6
14	1.09	4.7	27.3	0.0	6.9	58.5	0.0	2.6
16	1.21	4.7	17.4	59.8	2.3	3.1	12.7	0.0
17	1.59	20.9	31.0	5.8	9.7	5.5	27.1	0.0
18	1.43	4.1	14.8	21.0	2.4	46.7	11.0	0.0
20	1.67	22.7	11.8	0.0	14.0	23.4	24.6	3.5
26	1.80	9.8	12.1	11.9	13.1	34.6	12.3	6.2

*See Fig. 1.

Appendix 5 Brown bear diet composition, expressed as percentage of energy content (RE), and trophic diversity (Shannon–Wiener index, H').

Study area*	H'	Green vegetation	Fleshy fruits	Hard mast	Invertebrates	Vertebrates	Cereal bait	Others
1	1.13	27.5	20.5	0.0	2.7	49.3	0.0	0.0
2	0.15	1.0	2.0	0.0	0.0	97.0	0.0	0.0
3	1.19	36.9	19.2	0.0	4.2	39.7	0.0	0.0
4	1.16	16.6	36.6	0.0	4.3	42.5	0.0	0.0
5	1.31	10.1	25.0	0.0	32.4	32.5	0.0	0.0
7, 8	0.81	4.3	1.4	15.7	3.1	75.5	0.0	0.0
9, 10	1.21	4.9	8.9	54.5	5.7	26.0	0.0	0.0
12	0.99	4.2	31.4	0.0	6.3	58.1	0.0	0.0
13	1.30	7.8	17.0	0.0	12.6	62.6	0.0	0.0
14	0.70	1.4	14.7	0.0	5.7	78.2	0.0	0.0
16	1.11	2.5	13.9	66.3	2.8	4.5	10.0	0.0
17	1.69	12.1	29.0	7.5	13.7	12.4	25.3	0.0
18	1.13	1.6	9.2	18.2	1.5	62.7	6.8	0.0
20	1.45	12.0	9.1	0.0	16.3	43.7	18.9	0.0
26	1.37	4.1	8.0	11.0	13.1	55.7	8.1	0.0

*See Fig. 1.